EARLY STEM ANATOMY OF TODEA BARBARA

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(WITH PLATES XXIII–XXVI)

The work of JEFFREY (6) and FAULL (4) on the Osmundaceae, in which they interpreted the stele as containing a medulla of cortical origin, has stimulated an investigation into the condition of the stele as found in the ancestry of the line, and has brought forth a great deal of criticism.

The present investigation of the early sporophyte stages of *Todea barbara* was undertaken to ascertain whether in the early periods of organization and development there might be some phases which would be significant as to the ancestral stelar condition. Spores were sown, and from the resultant gametophytes large numbers of sporophytes were secured and examined in all stages of development up to the time of departure of the fourteenth leaf trace. Considerable variation appears in the development of the young sporophyte and in many of its anatomical features. This is especially true of the young plant before it has established its independence of the gametophyte. The first root, for instance, sometimes elongates first, breaking through the old venter wall, but more commonly the leaf takes this initial step. There is irregularity in the phyllotaxy of the first leaves, in the appearance and attachment of the first roots, in the appearance of sclerenchyma, and in the time of medullation.

The earliest protoxylem to appear has been observed to specialize opposite the foot attachment, where it continues downward in one of the two protoxylem points of the root, and upward into the stem, where it is associated with the elements which are diverted into the first trace. Part of the protoxylem elements of the second group in the root turn out and enter the foot region, while the others are oblique and are continuous into the basal portion of the stem, or may terminate at the junction of the foot and stem,

forming triaxial tracheae which are in contact at the three points with the tissues of the three plant regions.

The young stem directly above the foot attachment contains xylem elements which are relatively short and grouped in a typical protostelic manner. They are surrounded by a single layer of nucleated parenchyma cells, external to which a few sieve tubes are disposed in a much broken circle. These are succeeded externally by a pericycle layer one cell in width, and which, like the phloem, is more or less discontinuous. Frequently an embayment occurs in the xylem at the edge of the foot attachment with the stele (fig. 6). This is occupied by parenchyma which is usually continuous with that of the root which lies between the protoxylem points, and extends up into the stem, where it usually becomes more shallow, and is exserted before the departure of the first leaf or soon thereafter. This indention, when present, occurs at right angles to the plane of the foot attachment and never in the position of a gap (fig. 32).

The first leaf trace is detached from the stele about 70–150 μ above the foot, and is preceded by the appearance of 1–3 parenchyma cells in the xylem, which assume an eccentric position beneath the place of leaf exit. Quite commonly these first cells are in contact laterally with the sheath parenchyma; but whether in contact below or not, they become confluent with the sheath parenchyma at the time of exit of the first trace, when the xylem of the stele once more forms a solid group. It is quite evident, therefore, that this first xylem parenchyma is merely an accompanying feature of the departure of a simple trace from the protostele. Very similar to the preceding is an unusual behavior observed when an embayment of parenchyma at the foot attachment became decurrent in the xylem of the root. This parenchyma cell could not be shown to be in contact with that surrounding the xylem, but apparently was lost in the midst of the metaxylem elements of the root, just as the decurrent parenchyma associated with the departure of the early traces in the stem may end blindly in the tracheae a short distance below.

DeBary (3) considered the stele of the Osmundaceae as a sympodium of leaf traces, and, in reference to the young stem,

states: "The first bundle, which usually ends blind in the foot of the embryo, curves after a very short course through the stem into the first leaf; from the point of curvature the development of a bundle, which runs out into the second leaf, begins. In the case of the subsequent leaves the same conditions prevail." DEBARY'S interpretation of the stelar structures in this group has been supplanted by the theory of the stele as a unit in stem development (VAN TIEGHEM 12), which was strongly supported by GWYNNE-VAUGHAN'S (5) work on *Primula*, and subsequently by others, and which has at present gained most general credence. The conditions found in the young stem of *Todea barbara* give evidence in support of the later theory; for, as is readily observed, the trachea group above the foot is composed of 15–25 elements, while the number entering the first leaf is commonly but four, and was never observed to exceed six (fig. 5).

The stem axis bends at each node in the young sporophyte, so that the traces depart from the outer angles, a behavior undoubtedly referable to the manner of origin of the leaves, and is caused by pressure of segments cut off from the leaf apical cells and stem apical cells following the isolation of the former in a small meristem which has not yet become closely invested with leaf bases (figs. 35, 37). In the early organization of the stem a single apical cell appears, which is usually of the three-sided pyramidal type. Sometimes it is truncated at the base, and in most instances was found to be broader near the middle than at the top (fig. 36). Frequently, however, the apical cell is four-sided in transverse section (figs. 39, 41), and, like that of the root, cuts off segments more or less irregularly, often giving the appearance of a cluster of initials (figs. 38, 46). Only one instance of initials not certainly referable to a single cell was found (fig. 40). This instance occurred after the organization of the medulla, and appears to be a true case of more than one apical cell; but the earliest meristems were always referable to a single initial. At the level of departure of the first trace there is still a paucity of sieve cells (fig. 5); the pericycle is likewise incompletely developed, and, in fact, the feeble development of all the extra-xylar elements is quite noticeable in contrast with their relative prominence at higher levels in the

stem. The trachea elements of the early stele are strikingly uniform in caliber, pointed at the ends, relatively short, and display no certain delimitation of protoxylem and metaxylem.

Above the point of separation of the first and subsequent leaf traces a groove commonly occurs in the xylem axis directly opposite the departing strand (figs. 7, 9, 11, 15). This is continuous upward a variable distance, where it gradually becomes more shallow and disappears. Not infrequently, however, after the first one or two traces have departed, this groove may detach or be connected internally with a single parenchyma cell which passes up in the center of the trachea group, where it occasionally ends blindly, but more commonly becomes continuous with the sheath parenchyma once more through the embayment of decurrent parenchyma associated with the departure of the succeeding trace. Frequently such central parenchyma cells are in continuity externally through lateral embayments at the edge of root attachments, similar to that which occasionally accompanies the attachment of the foot. A leaf trace sometimes departs from the stele, which includes parenchyma decurrent from the trace above, without being accompanied by a break in the xylem cylinder.

In fig. 8 two included parenchyma cells appear, which are in contact with the sheath above (fig. 9). The embayment occurring opposite the departure of the second trace in this instance does not close up, but becomes continuous with that which isolates the third trace (figs. 10, 11). Above the third trace the protostele becomes divided in the plane of the exit of the last trace (fig. 12), but, contrary to expectation, neither segment is exserted as a trace, but the succeeding trace is detached from the segment to the right at a higher level (fig. 13). The two remaining strands fuse almost immediately, and subsequently an indention occurs opposite the last trace (figs. 14, 15). This is continuous with a group of two parenchyma cells which becomes centrally located (fig. 16), and is in contact with the sheath parenchyma again at the departure of the fifth trace (fig. 17). Reference to this series shows that five leaves take their departure from the stem before the organization of the second root, which appears directly beneath and is associated with the sixth leaf (fig. 18). The earliest phyllotaxy

in this instance is expressed by the fraction $\frac{2}{5}$. It later changes to a $\frac{3}{8}$ arrangement, which appeared most frequently in the early stem.

A solid protostele occurs a short distance above the fifth trace, and is illustrative of a constant recurrence of a perfectly solid stele associated with the departure of either the fifth or sixth foliar strand (fig. 18). The appearance of the protostele at the detachment of the fifth trace is shown in fig. 28, which is typical of this level of the stem in all of the young plants studied. It will be noted that the xylem is composed of tracheae alone, although internal parenchyma was present both above and below the three preceding nodes, and is constantly present above the level of the sixth trace. Although the occurrence of internodal parenchyma is common in the young stele, the number of elements is usually very limited. Occasionally, however, the internodal pocket becomes quite extensive (fig. 1), when the central cylinder assumes the appearance of a true siphonostele with centrally placed thin-walled elements. Yet despite the siphonostelic aspect, the stem becomes distinctly protostelic at the node above, and also at the level of exit of the fifth and sixth traces. The parenchyma pocket shown in fig. 16 is quite the normal condition, and is seen to be a basipetal extension from the cleavage of the stele at the node above.

It has already been pointed out that the departure of a trace from the protostele may so influence the xylem that it becomes entirely divided into two segments. A recurrence of this is shown in fig. 19, in which instance, however, the indentions of both the fifth and sixth traces are concerned, affecting the stele from opposite sides. The two residual strands coalesce immediately above the node as in the former instance cited (fig. 12). The eighth trace takes its departure from the stele in a similar manner to the fifth, leaving a solitary intruded parenchyma cell which is soon replaced above by tracheae, leaving a solid protostele (fig. 20). Even at nodal regions the stele was always observed to contain thin-walled elements above the level of the eighth leaf, while more commonly the fifth or sixth node marks the upper limit of a stele entirely free from these elements.

There is a gradual increase in the number of xylem elements accompanying the enlargement of the stem up to the time of

medullation (figs. 22, 23). In the change from the protostele to a siphonostele there is a rapid increase in the diameter of the stem, and an appearance of parenchyma cells with included resinous storage similar to those of the pericycle. These increase rapidly in number with the appearance of a permanent medulla, but so far as observed no real sclerenchyma of the type found in the adult stele occurred in young stems up to the time of the separation of the fourteenth leaf trace (fig. 24). This early organization of the medulla takes place without the appearance of internal phloem, nor could sieve cells be demonstrated at any level in the central parenchymatous elements of the young stele. It was further observed that there was no endodermal invagination accompanying medullation, or the departure of traces from the young stele, up to that time. True leaf gaps occur in the stele after the appearance of the medulla, and the traces take their departure in a manner already described by SINNOT (11).

The storage parenchyma cells already mentioned as being very prominent in the early medulla have been observed to occur as early as the time of separation of the third trace, but more commonly about the time the sixth trace leaves the central cylinder. The first elements of this character are usually located opposite the place of exit of a trace and appear free in the sheath parenchyma (fig. 2), or occur at the edge of a root attachment. In a few instances they have proved to be continuous with like elements of the pericycle layer, the storage contents of which cells they resemble. The most pronounced intrusion of such cells observed in any of the young stems is shown in fig. 44, where they occur opposite a trace and at the edge of a root attachment. In no instance, however, has it been possible to demonstrate any thickenings on the walls of these elements such as occur on the endodermis, and it seems that their relation to the pericycle is not at all constant.

The endodermis is organized early in the development of the sporophyte, and is continuous over the early stem, the primary root, and the tissues which elongate and diverge into the foot. At a comparatively early stage it closes over the conductive elements in the foot, and thus entirely incloses the stele from the root apices to the meristematic region of the stem apex. A transverse section

of the foot in a three-leaved sporophyte is shown in fig. 26, and it will be noticed that it almost caps the foot tissues at this early stage, only two cells remaining free. Throughout all the stages, so far as studied in the young stem, there was no indication whatever of the endodermis dipping into the stele; but in complete continuity it passes over the gaps in the xylem caused by the departing leaf traces, without the slightest tendency to invaginate. A commonly recurring feature of the endodermis from about the level of the sixth leaf trace was the absence of storage materials opposite leaf gaps. Frequently there was likewise an absence of storage in the pericycle at the same point. Across this gap in the storage material, however, the endodermis was always found to be continuous.

The origin of the pericycle from the stem apex is difficult to determine, and it could not be definitely referred to initials which would point to a common origin with the endodermis. For the most part the pericycle cells contain an abundance of finely granular resinous material. As has already been pointed out, the pericycle does not form a complete circle in the earliest stages of the stele, but is interrupted at many points. At the level of the sixth or eighth trace it is rarely more than one cell thick, and in the young sporophyte it seldom exceeds two cells in thickness except at the edge of root attachments and in the adaxial angle of the leaf traces, where it frequently becomes very prominent (figs. 3, 44), and, like the endodermis, is quite regularly filled with finely granular material or with larger granules similar to those of the storage cells in the sheath parenchyma and medulla. The pericycle is increased in thickness by periclinal divisions (fig. 1), but the so-called "quergestrickten Zellen" of the older stem which have their origin in this way do not appear prominently in the earliest stages, but appear much more abundantly after the development of a central medulla.

There is a paucity of sieve cells in the lower levels of the stele, where they are most prominently and regularly developed on the outer edge of the xylem elements which are about to turn out from the cylinder as traces. The sieve cells are elongated elements terminated by oblique walls. The radial, terminal, and likewise the

tangential walls when in contact with similar cells are perforated with openings which vary from simple pits to relatively large sieve plates with numerous small apertures. The transversely elongated elements derived from the pericycle by tangential divisions are, as pointed out by SEWARD and FORD (10), sieve elements which are of later origin than the sieve tubes of the protophloem. The sieve plates of these elements, as asserted by FAULL (4), show callus plugs, and all the essential features of true sieve cells are present. There was no evidence of the appearance of phloem in the internal parenchyma in any of the material investigated, nor were the sieve cells ever observed to appear in the parenchyma tissue of the foliar gaps.

As already stated, there is a single row of nucleated parenchyma cells which surround the xylem in the first stages of the stele. At higher levels these elements increase in amount by tangential divisions. In longitudinal view they are observed to be narrow, elongated, with acutely oblique terminal walls. These resemble very closely the earliest xylem parenchyma. Are these elements to be considered as of cortical origin, as asserted by JEFFREY (7) and FAULL (4), or are they to be considered as distinctly stelar and representing undeveloped potential xylem elements differentiated by the meristematic stem apex? In the young stele these cells do not resemble the cortical tissues either in topography or cytology. The central ones at first have distinctly acute terminal walls, and in general topography are altogether like the tracheae, except, of course, for the secondary thickenings of their walls. At higher levels these internal unthickened elements frequently have transverse terminal walls or are but slightly obliqued from the horizontal. Further evidence for the stelar origin of these elements is found in the occurrence of tracheids in the same linear series with parenchyma cells above and below (fig. 29). It was further noticed in such instances that the tracheids were terminated by walls which were transverse or almost so, instead of having the strongly oblique prosenchymatous type so characteristic of the normal tracheae of the xylem axis. Cells of this type were found on the inner edge of the xylem in contact with the parenchyma, and in a few instances on the outer border where

they were in contact with the sheath parenchyma. A first supposition that these were protoxylem elements was readily disproved; for the cells are continuous up the stem axis, and in no instance turned out into the diverging xylem group of the leaf traces, as do the protoxylem cells. Their squared terminal walls are likewise not characteristic of protoxylem as found in the stele and traces. They always were observed to include some cytoplasm and most frequently a degenerate nucleus. A transverse view of these cells is shown in fig. 27, where it will be noted that they have a thickening equal to that of the normal tracheae, and in conjunction with the true xylem elements do not develop the lacunae between cell walls except occasionally, when it is barely distinguishable. They also lack the angle thickenings so characteristic of the Osmundaceae. In view of their belated appearance, their topographical and cytological features, they are considered as abnormal tracheae, arrested in development, and are considered as evidence indicative of stelar origin of the medulla by reduction. SEWARD and FORD (10) referred to similar elements found in *T. superba* and *T. hymenophylloides*, and KIDSTON and GWYNNE-VAUGHAN (8) interpreted them as probably being vestigial. That these are the last remnants in our living species of the peculiar central xylem now known to have been present in *Kalesskya* (8) and *Thamnopteris* (9), extinct protostelic members of this family belonging to the Upper Permian, seems entirely probable, and is the most logical interpretation.

The primary root of the sporophyte, as well as the roots which appear successively with the development of leaves in the early plants, are characteristically diarch (occasionally triarch), with radially arranged phloem. A narrow zone of parenchyma separates the xylem and phloem in a manner similar to that in the young stem stele (fig. 43). Following the development of the first root, two or more leaves regularly occur before the appearance of the second. This in most instances is associated with the third or fourth leaf, but in a few cases it has been observed to appear considerably later. In the series represented by figs. 6–24 it will be noted that the second root is associated with the sixth leaf. Roots, following their delayed appearance, frequently develop in an aberrant manner, forming often without any particular

relation to departing traces. Leaves frequently develop without corresponding roots. This early vacillating condition is replaced by regularity after the establishment of a central parenchyma, and a single root takes its departure from the stele just below the attachment of the leaf trace. Subsequently there is a second period of irregularity when either one or two roots are detached from the stele with each leaf.

In his studies of the apical regions of *Todea barbara*, BOWER (1) states: "The roots take their origin from a single cell of the endodermis which is situated opposite a xylem strand." In all cases observed in the young stem the root apical cell originated in the pericycle (figs. 45, 48). The initial cell enlarges, and, following a few radial divisions, a single apical cell develops which is quite variable in shape, but very early organizes into a three-sided pyramidal cell (fig. 47). BOWER (1) further states that of a number of root apices examined in *Todea barbara* "not one showed a clearly marked single apical cell. Some, however, showed somewhat irregular arrangements, and in some it appeared uncertain whether the meristem be referable to three or four initial cells. In the majority of the roots observed it is clearly referable to four initial cells, separated from each other by the four principal walls." In examining the root meristems in the young plants of *Todea barbara*, 28 single apical initials were recorded in as many different plants, and not a single instance of four initials was observed. There were a few cases which showed some variation from the pyramidal three-sided cell, with the divisions occurring unevenly. The segments from the apical cell are usually very large and do not divide immediately, resulting in a meristematic group resembling in longitudinal view a cluster of three or four initials. These, however, have always been referable in the root to a single initial which was prevailingly of the triangular-pyramidal variety. Thus the coaxial type described by BOWER (1) was not found in any of the root meristems of the early sporophytes.

The outer cortical cells of the primary root are usually the first to develop the sclerenchyma thickenings which later become so conspicuous a feature of the stem cortex. From the primary root they are extended to the adjoining cells of the stem in which

they persist throughout the axis. Frequently, however, the lower portion of the stem cortex is free from sclerenchyma, in which instance it is found to appear in the stem at the place of attachment of the second root, from the base of which it extends about the stele. When it first appears in this manner, the petioles of the leaves below the point of introduction most generally lack the characteristic cortical wall thickening of the cells surrounding the central bundle. After its first appearance in the stem it is sparingly developed or absent from the base of the next one or two petioles, although quite abundant in the stem axis and the leaves at higher levels, which would indicate that the rachis has been the last region of the plant to develop the sclerenchyma. An endophytic fungus was found to occur frequently in the cortical tissues of the root, external to the endodermis and internal to the sclerenchymatous cells of the peripheral region. It was found to gain entrance by way of root hairs, and also by dissolving its way through the epidermal cell wall at the edge of the root cap (fig. 42).

The first leaf originates at a point about 0.1 mm. above the foot attachment. The trace is isolated by an embayment, and carries off from the main axis about four cells (varies from three to six), which usually form a narrow band (fig. 5) which, once in the petiole, usually becomes endarch in its arrangement (fig. 33). Subsequent traces depart in a similar manner, carrying out an increasingly greater number of xylem elements until the appearance of a definite medulla tissue. The first petioles are practically wingless, but with an increase in leaf size and number they overlap and become conspicuously winged. The metaxylem elements meanwhile become more numerous, spreading out so as to form a semicircle with the opening toward the stele (fig. 34). The poorly defined phloem of the first trace becomes more definite and abundant in the second and third, where it may form a complete circle about the xylem.

In the petioles of the lower leaves the xylem sometimes assumes a distinctly mesarch arrangement, but is not completely invested by phloem (figs. 4, 25). The occurrence of primitive structures in the basal petioles has long been recognized, and the appearance of mesarch strands here is further evidence for the origin of our

present Osmundaceae from a protostelic group. It becomes particularly significant when we observe that *Kalesskya* and *Thamnopteris* were characterized by traces which departed in a protostelic manner and were strongly mesarch until they had entered for some distance into the petioles, where the xylem opened out and presented an appearance like that in the rachis of *Osmunda* and *Todea*. As already stated, these early representatives of the Osmundaceae were present in the Upper Permian and much preceded the Lower Cretaceous siphonostelic species *Osmundites skidegatensis* to which JEFFREY (7) referred for the most primitive type of osmundaceous stele available. The recurrence of mesarch strands, abnormal central tracheids, and a typical protostele in the young stem of *Todea* are interpreted as indicative of the descent of our present Osmundaceae from a protostelic ancestry.

Summary

1. The young sporophyte of *Todea barbara* is protostelic.

2. Preceding the departure of the early traces one or more parenchyma cells appear in the xylem group, or occupy a groove which is in contact with the sheath parenchyma. These, at the time of isolation of the trace from the central cylinder, become confluent with the xylem sheath, leaving the stele solid, or grooved opposite the strand. This depression is continuous up the stem, where it either becomes more shallow and is lost, or detaches one or more parenchyma elements which become centrally placed in the xylem group where they end blindly, or are in continuity with parenchyma decurrent from the succeeding trace.

3. The stem meristematic tissue is derived from a single apical cell of the triangular-pyramidal type. It, like the root initial, shows variation in the order of segmentation. Only one instance not certainly referable to a single initial was found.

4. Roots originate from the pericycle in the young sporophyte and very early develop a single apical cell which is broadly triangular and pyramidal, characterized by variation in shape and order of segmentation. Segments are large and frequently give the appearance of two or more apical initials. All root meristems examined, however, were referable to a single initial.

5. The cortical sclerenchyma is apparently of root origin, and is extended to the stem cortex from the primary root or from those which develop later in association with leaves.

6. An endophytic fungus is frequently found in the root cortex. It was observed to gain entrance through root hairs and through newly formed epidermis at the edge of the root cap.

7. A phyllotaxy represented by the fraction $\frac{3}{8}$ is most frequently found in the young plant. A $\frac{2}{5}$ arrangement was recorded in addition to a few cases of irregularity.

8. Leaf traces usually are endarch while in the stem cortex, and the protoxylem elements, which at first form a narrow band, spread out on the adaxial embayment which occurs in the metaxylem higher up in the petiole of the leaves.

9. Typical mesarch bundles have been observed in the petioles of early leaves. These are interpreted as being indicative of the ancestral condition, and in fact present the type of arrangement found by KIDSTON and GWYNNE-VAUGHAN to be characteristic of *Kalesskya* and *Thamnopteris*, Upper Permian representatives of this family.

10. The transversely elongated phloem elements are derived from periclinal divisions of the pericycle, and, as recorded by SEWARD and FORD, are sieve tubes which, in the organization of the stele, appear considerably later than the protophloem.

11. No instance of phloem within the medulla or central parenchyma was found at any level in the young stele.

12. The endodermis is continuous over the primary root, foot, and early stem. At no place in the young stem does it turn in through the gaps or embayments in the xylem.

13. Internal endodermis could not be demonstrated at any stage in the young stele.

14. The earliest parenchyma to appear within the xylem is composed of elements with pointed ends, whose caliber and length are very similar to the xylem elements, and conspicuously unlike the cortical cells.

15. No sclerenchyma was observed in the medulla up to the time of departure of the fourteenth leaf trace, although parenchyma cells with included resinous substances were quite abundant.

16. After the first organization of a definite medulla, short, thickened xylem cells have been observed to be present on the inner edge adjoining the pith. These elements, although thickened, were poorly lignified, contained some protoplasm and a degenerate nucleus, had transverse or slightly obliqued terminal walls, were usually in axial continuity above or below with parenchyma elements, and when in contact with adjoining tracheae did not develop the intercellular lacunae so characteristic of the protoxylem and metaxylem of this family. These elements are considered as belated xylem of vestigial character, and, because of their position and relation to the internal parenchyma, are evidence of medullary origin by stelar reduction. Cells of this type were not found in either the petiole or root.

17. The appearance of mesarch traces in basal leaves, a protostele in the early stem, the similarity in topography of early xylem parenchyma to xylem, the appearance on the inner border of the xylem of peculiar short tracheids with transverse terminal walls, the entire absence of internal phloem, the absence of internal endodermis, and the complete unity of the endodermis (which shows no indication of invagination) are all features in the ontogeny of *Todea barbara* which are indicative of a protostelic ancestry. These features assume a special significance when we can correlate them with similar structures in primitive forms, and their recurrence in *Kalesskya* and *Thamnopteris* further validates the theory of the protostelic origin of our living Osmundaceae.

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EXPLANATION OF PLATES XXIII–XXVI

PLATE XXIII

FIG. 1.—Transverse section of stele between third and fourth traces, showing extensive parenchyma pocket and periclinal divisions of pericycle; ×300.

FIG. 2.—Stele with tenth trace and seventh root; storage parenchyma in xylem sheath opposite trace, and three xylem parenchyma cells; ×88.

FIG. 3.—Transverse section of stele and seventh root; absence of storage in endodermis and pericycle opposite trace; gaps of sixth and seventh leaves; extensive pericycle development opposite sixth trace; ×138.

FIG. 4.—Mesarch grouping of xylem elements in petiole of third leaf, $\frac{1}{3}$ mm. above separation from stele; ×118.

FIG. 5.—Transverse section of stele and first trace, showing early phloem cells and paucity of extra-xylar elements in stelar cylinder; ×58.

PLATE XXIV

FIGS. 6–24 inclusive, ×40 diameter.

FIG. 6.—Foot attachment and lateral embayment of parenchyma.

FIG. 7.—First trace and grooving of xylem opposite.

FIG. 8.—Xylem with two parenchyma elements included.

FIG. 9.—Separation of second trace and grooving of xylem.

FIGS. 10, 11.—Separation of third trace from stele.

FIG. 12.—Cleavage of protostele into two strands.

FIG. 13.—Fourth trace being isolated from strand to right.

FIGS. 14–16.—Embayment and inclosure of parenchyma elements preliminary to detachment of fifth trace.

FIG. 17.—Connection of parenchyma of preceding figure with that of xylem sheath at time of separation of fifth trace.

FIG. 18.—Solid protostele above fifth trace; first root detached immediately below this level at lower left.

FIG. 19.—Second cleavage of protostele, with seventh trace to right.

FIG. 20.—Solid protostele with detached tracheae, decurrent from root which leaves stele immediately above.

FIG. 21.—Enlarged xylem group just before medullation.

FIG. 22.—Early medullation and inclusion of first storage parenchyma cells; eleventh trace.

FIG. 23.—Twelfth trace and eighth root.

FIG. 24.—Increase in storage parenchyma cells and medulla; ninth root.

PLATE XXV

FIG. 25.—Mesarch bundle in petiole of first leaf; ×625.

FIG. 26.—Transverse section of foot, showing closing of endodermis in three-leaved stage; ×88.

FIG. 27.—Transverse section of abnormal tracheids; ×625.

FIG. 28.—Stele at time of departure of fifth trace, showing solid xylem group and prominent sheath parenchyma; ×300.

FIG. 29.—Longitudinal section of tracheid in axial continuity with xylem parenchyma cells; ×300.

FIGS. 30, 31.—Sieve tubes with oblique terminal walls; ×300.

FIG. 32.—Stele immediately above foot; lateral embayment to right of foot attachment and indention of stele to isolate first trace at left; ×300.

FIG. 33.—Normal endarch bundle of first trace; ×88.

FIG. 34.—Fifth leaf strand 2.25 mm. above origin; phloem encircles xylem which shows adaxial embayment; ×300.

PLATE XXVI

FIG. 35.—Stem apical cell with leaf initial isolated at left; ×300.

FIG. 36.—Longitudinal view of stem apical cell; ×575.

FIG. 37.—Isolation of leaf initial from stem apical cell; ×575.

FIGS. 38, 39.—Irregularity in segmentation of stem apical cell; ×575.

FIG. 40.—Abnormal meristem with apparently four initials; ×300.

FIG. 41.—Transverse view of normal stem apical cell; ×129.

FIG. 42.—Cortical cell of root with endophytic fungus; ×625.

FIG. 43.—Transverse section of normal root, showing diarch character; ×88.

FIG. 44.—Transverse section of stem, showing at left a pericyclic intrusion and strong development at edge of root attachment; ×88.

FIG. 45.—Longitudinal section of root apical initial in pericycle; ×300.

FIG. 46.—Irregular segmentation of root apical cell; ×575.

FIG. 47.—Transverse section of triangular-pyramidal root apical cell; ×300.

FIG. 48.—Tangential section of stele, showing organization of root apex in pericycle; ×300.